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ON FACILITATION BETWEEN HERBIVORES: HOW BRENT GEESE PROFIT FROM BROWN HARES

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Abstract. Brown hares (*Lepus europaeus*) are shown to facilitate grazing by Brent Geese (*Branta bernicla*) in a temperate salt marsh in the Netherlands by retarding vegetation succession for >25 yr. Winter grazing by hares prevented the shrub *Atriplex portulacoides* from spreading in younger parts of the salt marsh. Clipping experiments showed that *Atriplex* had poor recovery after removal of aboveground tissue, which makes *Atriplex* vulnerable for hare attack. Once *Atriplex* swards were cut to the ground to mimic hare grazing, Brent Geese visited those sites more than twice as frequently than untouched control plots. Goose visitation was reduced when bushes of *Atriplex* were planted. Large parts of the core feeding area of Brent Geese would be unsuitable for goose grazing if hares were not present. A reduction of at least 44% in the carrying capacity of the marsh for Brent Geese was calculated in the absence of hares. Vulnerability of *Atriplex* to hare grazing and the high food intake of geese are key elements to this facilitative pattern. Additionally, hares reduced the number of dead *Artemisia maritima* stems in grassy swards, which otherwise might have hampered grazing by geese. Facilitation by herbivores such as hare, rabbit, cattle, and sheep is likely to be a prominent factor enhancing feeding conditions for Brent Geese all along the northwest European coast.

Key words: Branta bernicla; *Brent Goose; brown hare; competition; facilitation; herbivores;* Lepus europaeus; *Netherlands; salt marsh; shrub.*

INTRODUCTION

Interactions among species are regarded as crucial to the functioning of ecosystems (Paine 1980). Many theoretical and field ecologists have emphasized the importance of negative, competitive interactions among animal species in structuring communities (Schoener 1974, 1983, Connell 1983, Belovsky 1984, Hairston 1989). Positive, facilitative interactions among animal species, however, have gained less attention (Damman 1989, Hairston 1989). Facilitation occurs when one species has a beneficial effect upon another species.

Here we focus on the process of facilitation between herbivorous species. Although facilitation is claimed to be important in many systems, published information on both interacting members is scarce. One might expect facilitation to be most pronounced in East Africa, where, in some cases, >15 species of larger herbivores live sympatrically, and where overall herbivore density is high. But very little evidence for facilitation among herbivores has been found there (De Boer and Prins 1990, Prins and Olff 1998). Facilitation has been suggested to be the driving force in grazing succession of ungulates in the Serengeti, where grazers arriving first on a site are thought to prepare the structure of the vegetation for later arriving grazers (Vesey-Fitzgerald 1960, Bell 1971). With the exception of Thomson's gazelle (*Gazella thomsonii*) benefiting from wildebeest (*Connochaetes taurinus*) grazing in some years (McNaughton 1976, but see Sinclair and Norton-Griffiths 1982), there is very little evidence that later members of the grazing succession actually followed earlier ones because of enhanced feeding opportunities (Sinclair and Norton-Griffiths 1982, De Boer and Prins 1990). Also, mechanisms proposed in the 1970s involved in grazing succession are still being debated (Illius and Gordon 1987). This is not to say that facilitation among herbivores is absent, however. Other studies have shown that facilitative processes do operate in marine (e.g., Dethier and Duggins 1984), freshwater (Brönmark et al. 1991), and terrestrial systems (e.g., Gordon 1988), and across a large range of body sizes (Viejo and Arrontes 1992 [isopod], Eltringham 1974 [hippopotamus]).

In the present study we report on brown hare (*Lepus europaeus*) facilitating grazing by dark-bellied Brent Geese (*Branta bernicla bernicla*) in a temperate salt marsh in the Netherlands. Because this system is relatively simple, with a limited number of plant species, few (vertebrate) herbivores, and virtually no predators, we were able to use an experimental approach to un-

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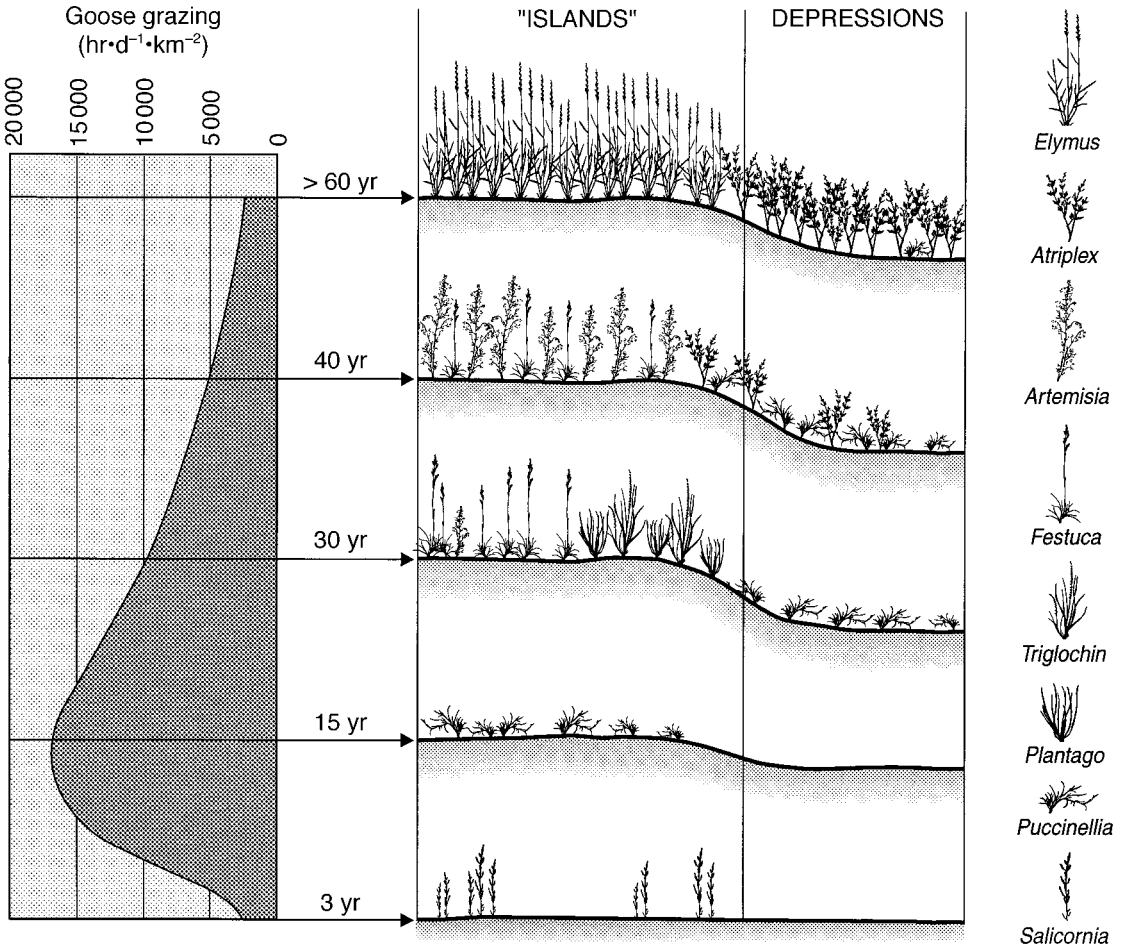

FIG. 1. Changes in vegetation composition over time, and use of the differently aged parts of the salt marsh by Brent Geese. Young marshes are sparsely vegetated, while tall growing plants dominate in older marshes. During vegetation succession, food plants of Brent Geese (*Puccinellia, Festuca, Triglochin, Plantago*) largely disappear. Data on geese originate from repeated day-long observations on number of birds in marshes of 15, 30, and 40 yr of developmental age.

ravel interactions between the species involved. We focus on (potential) effects of hare grazing on two common dwarf shrubs *Artemisia maritima* and *Atriplex portulacoides* (formerly called *Halimione portulacoides*), which were expected to hamper goose grazing when reaching dominance. Habitat use of hare and Brent Goose was quantified, and the herbivores' effect upon the vegetation was measured using exclosures. The impact of hare grazing on *Artemisia* and *Atriplex* was simulated by performing clipping experiments, and we measured response by geese to manipulated shrub occurence. We also discuss the importance of the process of facilitation for the carrying capacity of the northwest European coast for Brent Geese.

METHODS

Study area

The study was performed in a salt marsh on the island of Schiermonnikoog, the Netherlands (53°30′ N, 6°18′ E). One characteristic of this salt marsh is that it represents a clear successional sequence, caused by ongoing sedimentation of silt associated with inundation by sea water, which provides nutrients necessary for plant growth (Olff et al. 1997, Van Wijnen and Bakker 1997). Over time, initially bare sandy flats become vegetated, and a dense vegetation is found in sections of the marsh older than ~40 yr, where the clay layer is >10 cm thick. See Olff et al. (1997) for a detailed description of the successional sequence.

We will focus on the low-lying marsh which is frequently inundated by sea water, and forms the key feeding area of Brent Geese (Prop and Deerenberg 1991). This lower marsh is patchy and characterized by a mosaic of small elevated areas (''islands'') separated by shallow depressions. During vegetation succession, elevated parts change from a sparse vegetation dominated by *Puccinellia maritima* and *Spergularia maritima* into dense mixed swards of *Festuca rubra* and *Artemisia maritima.* Eventually tall-growing *Elymus athericus* invades and will dominate the vegetation (Fig. 1; Bakker

et al. 1997). In depressions, vegetation is sparse for a much longer time. *Puccinellia*, dominant in the early phase, will eventually be overgrown by *Atriplex portulacoides* (Fig. 1). The highly preferred food plants of Brent Geese, *Plantago maritima* and *Triglochin maritima*, grow in the younger marsh on shallow slopes of those islands (Prop and Deerenberg 1991). Names of plant species are in accordance with Van der Meijden et al. (1990).

Brent Geese visit marshes in April and May to fatten up for spring migration (Ebbinge and Spaans 1995). Grazing pressure of geese is greatest in salt marshes of intermediate age (Fig. 1), where total plant cover is low, but the proportion of palatable plant species is high (van der Wal et al. 2000). Older salt marshes dominated by *Elymus athericus* are unsuitable for grazing by Brent Geese (Olff et al. 1997). Additionally, presence of *Atriplex portulacoides* and *Artemisia maritima* (hereafter called *Atriplex* and *Artemisia*, respectively) reduces goose utilization (Drent and Van der Wal 1999). After invasion of both woody species in one key feeding area of Brent Geese in the late 1970s, grazing pressure dropped by >60% from 3343 ± 751 goose hours per day (mean ± 1 SE) in 1979 to 1197 ± 198 goose hours per day in 1994 (Bakker et al. 1997).

Hares largely overlap with Brent Geese in use of different successional stages (Van de Koppel et al. 1996). Hares are resident herbivores, grazing in both dune and marsh areas. Autumn counts revealed that hare density was high (1 hare/ha; R. van der Wal, *personal observation*). Despite large fluctuations in food availability, due to both flooding and seasonality, no large-scale movements of radio-tagged hare have been observed (S. van Wieren, *unpublished data*). Individuals were faithful to their home ranges of <35 ha throughout the year.

Rabbit (*Oryctolagus cuniculus*) grazing is expected to be of very limited importance in this study. Because of their close association with dunes, rabbits graze only in the upper part of the salt marsh (R. van der Wal, *unpublished data*). Similarly, staging by Barnacle Geese (*Branta leucopsis*) in spring and autumn is relatively unimportant to our study, because of their strong preference for the upper marsh (Ydenberg and Prins 1981).

Diet of hares

Diet composition of hares was established by means of fecal analysis (Stewart 1967). Droppings were collected every other week in two areas during the periods February 1996–May 1996 and December 1996–January 1997. In the youngest area we studied (±15-yr-old marsh), droppings were collected in twenty 2.5-m^2 plots evenly distributed over the four most common vegetation types, following a stratified sampling design in which vegetation types were selected for, but actual plots were laid out randomly within a vegetation type. In the oldest area (±40 yr old), droppings were collected in 30 similarly sized plots, distributed over six vegetation types. For every collection date, droppings of each area were pooled. A subsample of this pooled material was blended, and washed over a 0.1-mm plankton sieve to facilitate recognition of epidermal fragments under a microscope. In each sample, we measured surface area of 100 fragments encountered in marked tracks, and determined fragments to species level using an extensive reference collection. Repeatability among trials within a sample was found to be >90%, indicating that substantial changes in diet were likely to be detected. Less than 3% of all fragments could not be identified.

Effects of hare grazing on shrubs

Three small exclosures (2 × 4 m) were erected in autumn 1991, one each in a 15-, 30-, and 40-yr-old part of the marsh. Twelve larger ones were erected in spring 1994, all distributed over four areas of ~5 (2 exclosures), 15 (4 exclosures), 30 (4 exclosures), and 40 (2 exclosures) yr of developmental age. The 12 larger exclosures were composed of two compartments with adjacent controls. In one compartment (~5 × 8 m), both hare and geese were effectively fenced out by a combination of sheep and chicken wire. In a second compartment (~5 × 5 m), geese were fenced out while hares could freely enter. Geese were kept out by two lines of metal wire at ~20 and 50 cm height, nailed to a set of wooden poles. All grazers had free access to the control plots (~5 × 5 m).

In all 12 exclosures erected in 1994, canopy height was measured in May 1996 by letting a small styrofoam disk (6 cm in diameter, 16 g) slide along a thin graduated stick and come to rest on the vegetation. To avoid pseudoreplication, the average of the 100 randomly taken measurements per treatment per exclosure was used to test for differences in canopy height among the three grazing treatments by means of one-way ANOVA, employing Tukey HSD contrasts.

Abundance of *Atriplex* and *Artemisia* was recorded in mid-June by means of visual cover estimates in permanent plots marked out in all three exclosures built in 1991, and in 8 (out of 12) exclosures built in 1994. All of those exclosures were positioned in the lower marsh, ~40 cm above mean high tide (MHT). For graphical presentation, data for all permanent plots are given (2–4 plots·[treatment]$^{-1}$·[exclosure]$^{-1}$), unless elevation of a plot was too high for *Atriplex* and *Artemisia* to occur. These higher-elevation plots were covered with dense grass tussocks. For statistical analysis, however, data from all permanent quadrats in a single exclosure were averaged to avoid pseudoreplication. We tested for differences in abundance during the study by comparing initial (1994) cover estimates with final (1997) values. Because plant cover estimates were collected by different people in different years, we used a crude method to analyze the data by looking at substantial changes only. A plant species was said to in-

TABLE 1. Results of clipping experiments and hare browsing on (A) *Artemisia* and (B) *Atriplex.*

Plant stature	Treatment	Date of grazing/clipping	*n*	Grazed/clipped	Control	Test	*P*≤
A) *Artemisia maritima*							
Biomass							
Dense bush	hare grazed	winter 1996	8	403 ± 59	309 ± 85	WMP†	0.05
Resprouting							
Single shoot	clipped	27 February 1996	···	43 out of 49	16 out of 17	χ^2 test	NS
Single shoot	clipped	12 April 1996	···	14 out of 23	19 out of 24	χ^2 test	NS
B) *Atriplex portulacoides*							
Biomass							
Dense bush	hare grazed	winter 1996	8	422 ± 208	674.5 ± 390.8	WMP	0.05
Dense bush	clipped	24 March 1997	5	7 ± 12	569.2 ± 182.7	WMP	0.05
Resprouting							
Single shoot	clipped	27 February 1996	···	18 out of 25	21 out of 21	χ^2 test	NS
Single shoot	clipped	12 April 1996	···	12 out of 24	21 out of 24	χ^2 test	NS
Survival							
Whole young plant	clipped	21 March 1997	···	4 out of 20	18 out of 20	χ^2 test	NS
Whole young plant	clipped	7 April 1997	···	0 out of 10	10 out of 10	χ^2 test	NS

Notes: Live biomass (g dry mass/m^2) is given where dense bushes were either clipped or hare grazed. Response of shoots or plants is given for data on resprouting and survival. For instance, 43 out of 49 means that 43 out of 49 clipped plants resprouted, whereas 16 out of 17 control plants resprouted.

† WMP = Wilcoxon matched-pairs test.

crease when recorded plant cover more than doubled from the initial to the final years. Analogously, a plant species was said to decrease when estimated plant cover in the final year was half that of the initial year. All other cases were treated as if no substantial changes had occurred. We used χ^2 tests to judge whether occurrence of substantial changes in plant species abundance differed between the two types of exclosures and controls. Contingency tables, therefore, have six cells (treatment vs. control × three possible levels of change).

In all cases where the vegetation was dominated by *Limonium vulgare,* exclusion of hares led to an increase in *Atriplex.* Areas dominated by *Limonium* were mapped in the field in June 1996, aided by false-color photographs. Communities already dominated by *Atriplex* were mapped at the same time (mean cover of *Atriplex*: 56%). Our estimate is conservative because exclosures were not built in all relevant plant communities to test for grazing effects on plant species composition.

To describe the distribution of *Atriplex* along the successional gradient in the natural situation (with both hares and geese present), we used a detailed vegetation map of the salt marsh from 1996 where *Atriplex* cover had been estimated on each map unit. Only areas larger than 5 × 5 m were mapped. From ~50 sites on the map, evenly distributed over the marsh and with an elevation between 20 and 40 cm +MHT, we estimated both marsh age and *Atriplex* cover. A response curve was calculated, using the equation $Y = M[1 + \exp(a + b \times X)]$, where Y was *Atriplex* cover, M was maximum cover, a and b were estimated parameters, and X was the age of the marsh.

Effects of hare grazing on plant regrowth and survival

To estimate the ability of *Atriplex* and *Artemisia* to recover from hare browsing, we performed clipping experiments and monitored sites where hares grazed down plants themselves. In all experiments, pairs of experimental vs. control plots were laid out, allowing pairwise testing with Wilcoxon matched-pairs tests.

In spring 1996, eight widely spaced clearings created by hares in swards previously dominated by either *Atriplex* or *Artemisia* were selected. *Atriplex* plants had been severely browsed leaving a stubble of a few centimeters, while *Artemisia* plants had been bitten off at various heights. Control plots without signs of hare grazing were laid out in the same area. By the middle of June 1996, aboveground biomass was sampled in all experimental and control plots (36 × 36 cm per plot), dried for 36 h at 70°C, and weighed.

Single shoots of *Artemisia* growing in a 25 yr old *Festuca*/*Artemisia*-dominated marsh were clipped at 2 cm height on two dates in spring (see Table 1 for more details). *Atriplex* plants involved in clipping experiments differed largely in size and probably age. In a 5-yr-old part of the marsh, solitary plants of ~2 yr old (±10 cm high, mostly single branched) growing in *Spartina anglica* tussocks were clipped to 1 cm height in late March. Survival was recorded in the last week of October. Separately growing *Atriplex* bushes of ~20 cm diameter in a 35-yr-old section of the marsh were clipped to 1 cm height early in April. Survival of all clipped and control *Atriplex* plants was measured in the last week of October. In a 35-yr-old marsh, single shoots of multibranched plants also were clipped in

February or April. Resprouting was checked regularly until early June. Squares of 25 × 25 cm were cut out of dense *Atriplex* bushes in a 40-yr-old marsh. Regrowth was harvested in October, together with the control plots. From clipping experiments performed in 1997 (see Table 1), the proportion of aboveground to total *Atriplex* biomass was estimated in October 1997.

Brent Goose grazing pressure

To test whether hare grazing affected feeding opportunities for Brent Geese, we performed two experiments. In the first experiment, we removed *Atriplex* and measured goose response in terms of dropping density, which is commonly regarded as an index for grazing pressure by geese (Owen 1971). In a second experiment, we planted *Atriplex* and subsequently counted number of goose droppings in both the planted and control areas.

In the first experiment, 25 plots were laid out in the last week of March 1997, equally distributed over five areas where *Atriplex* cover was high. Hare grazing was mimicked by cutting down all *Atriplex* shoots to ground level in 1 × 1 m plots. Control plots were marked out pairwise with small plastic sticks. We regularly found similar patches of *Atriplex* grazed down to soil surface by hares, indicating that our treatment was ecologically sound. Every week, goose droppings were counted and removed from both experimental and control plots. The experiment lasted until 27 May, when all Brent Geese had left the island to migrate to the breeding grounds. We analyzed cumulative number of droppings per plot, using Wilcoxon matched-pairs test (WMP).

In the second experiment, 10 *Atriplex* bushes were constructed in the young salt marsh (~15 yr old), all on sites that were intensively used by Brent Geese. In that area, natural *Atriplex* cover was very low, with only some prostrate plants growing on creek banks. *Atriplex* shoots were collected in the 40-yr-old marsh and transported to the young marsh where branches were placed in soil creating bushes of natural stature and density. The first bush planted in the last week of March 1997 was grazed down to the ground by hares within four days and hence was not of any further use for the experiment. The other nine bushes were planted three weeks later; these were only lightly browsed by hares. Bushes were circular shaped, covering an area of 1 m^2. Droppings were collected in a larger area of 4 m^2, including the area covered by the bush. The experiment lasted until 27 May 1997. Cumulative number of droppings were analyzed with Wilcoxon matched-pairs tests, comparing plots in which *Atriplex* was planted with control plots.

Spatial distribution of Brent Geese in spring was determined by executing a weekly census from observation points with known position. Censuses were done by foot with alternating direction of travel between weeks, covering the whole salt marsh. Using a rangefinder (Leica Geovid 7 × 42), the geographical position of the center of each group observed was assessed by measuring distance and angle between observer and group or individual goose. A group was defined as a cluster of geese, separated from other geese by ≥50 m, or foraging on a different vegetation type than other geese present. The data were entered in a Geographical Information System (GIS) and the percentage of all birds in each of the discriminated vegetation types was determined by making an overlay of goose data on the vegetation map.

RESULTS

Diet of hares

We found marked differences in diet of hares between the 15-yr and 40-yr-old marsh. During winter, monocots dominated the diet of hares in the young marsh, whereas the dicot *Atriplex* was the most common food item of hares in the older marsh (Fig. 2). This was confirmed by fecal material collected in February 1994 (old marsh), in which 50% of fragments were recognized as *Atriplex.* From mid-April onwards, differences between the two areas were waning. In spring, *Festuca* became increasingly important; at the end of May ~70% of the diet was composed of that grass in both areas. Similar values for *Festuca* were found in October and November 1993 (R. van der Wal, *unpublished data*), making it likely that *Festuca* is the most important food plant for hares during most of the year. The incidence of *Artemisia* in fecal material was low: 1.8 ± 1.6% vs 1.4 ± 1.7% in the 15-yr-old and 40-yr-old marsh, respectively, and therefore not explicitly presented in Fig. 2.

Effects of hare grazing on shrubs

Abundance of *Atriplex* in the diet of hares in winter and early spring matches with the occurrence of clearings in the field, all of different size up to >25 m^2. The first clearings in *Atriplex*-dominated vegetation types were observed in December. In such clearings, nearly all woody above-ground *Atriplex* parts were consumed by hares, leaving behind only fallen leaves, small branches, and numerous hare droppings.

After 3–5 yr of exclusion, *Atriplex* cover increased in many permanent plots, whereas no increase was observed in control areas grazed by both hare and geese (Fig. 3: compare panel A with B; $\chi^2_2 = 10.6$, $P < 0.01$). Exclusion of geese alone did not influence *Atriplex* cover (Fig. 3C; $\chi^2_2 = 2.6$, NS). Therefore, *Atriplex* cover is expected to be high in the absence of hares in salt marshes ~15 yr old, whereas in marshes grazed by hares, *Atriplex* becomes dominant ~25 yr later (Fig. 3A, dashed vs. straight line). In autumn 1996 three exclosures established in 1991 were dismantled to expose vegetation to hares. In those plots *Atriplex* cover was strongly reduced within a single winter from an average of 25% to only 0.6%. Maximum *Atriplex* abundance changed from >50% in exclosures to ≤3% after opening them.

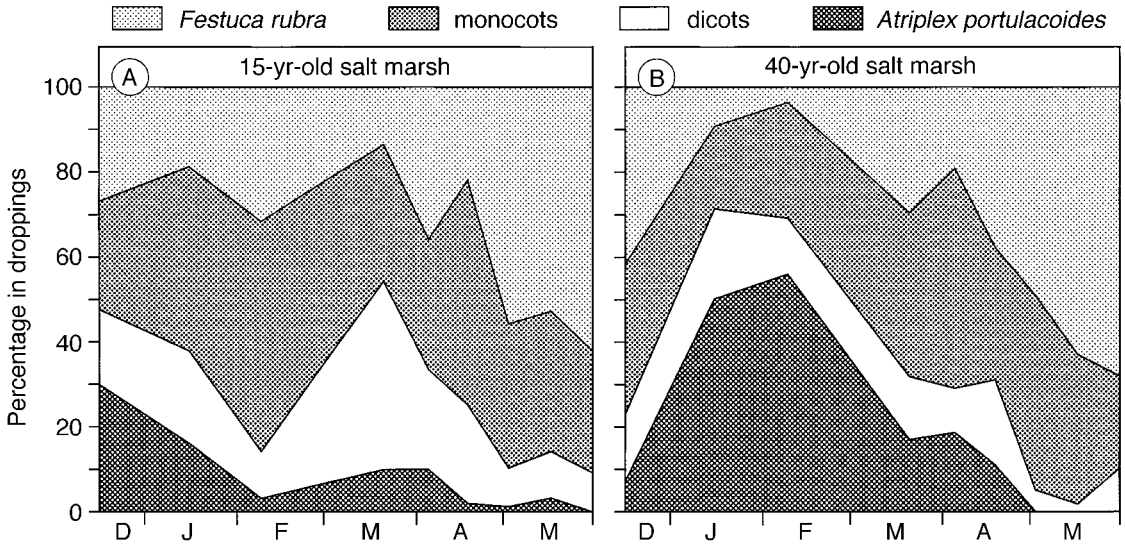

FIG. 2. Diet composition of hares during winter and spring in (A) a 15-yr-old and (B) a 40-yr-old part of the marsh. Note the use of *Atriplex* during winter in both parts of the marsh.

Abundance of *Artemisia* in exclosures, as measured during summer, was not significantly different from that in the control plots ($\chi^2 = 3.9$, NS). However, *Artemisia* was grazed by hares. We observed clearings as early as November, while fresh clearings were found as late as March. Clearings were characterized by numerous *Artemisia* stems lying loose on the marsh floor. Stems were cut down at various heights, with stubble rising 0–5 cm out of the grass carpet. Forming the tallest plant parts, presence of the previous years' stems of *Artemisia* largely influenced canopy height of swards dominated by either *Festuca rubra* or *Artemisia* in spring. Canopy height was significantly reduced by grazing (*Festuca*, $F_{2,19} = 6.48$, $P < 0.01$; *Artemisia*, $F_{2,17} = 21.10$, $P < 0.001$). Plots accessible to hares had lower canopy height than plots free from hare grazing, irrespective of the presence of geese (Fig. 4). This means that in spring, Brent Geese face a sward largely devoid of *Artemisia* stems due to hare grazing earlier in the season, which may enhance food intake rate by geese.

Effects of hare grazing on plant regrowth and survival

In preparation for winter, *Atriplex* stores a large proportion of total nutrients in live above-ground tissue. That allocation pattern changed with plant size or age. Young plants (<2 yr) growing in the 5-yr-old marsh, had 85 ± 7% (mean ± 1 SD) of their total plant biomass in above-ground tissue, whereas this was 70 ± 7% in mature plants growing in separated clones in a 30-yr-old marsh. In dense monocultures in the 40-yr-old marsh, 42 ± 14% of the total plant biomass was allocated above ground. In *Artemisia* most of the above-ground parts die off, and only the lower 30% of the remaining woody stem is alive (R. van der Wal, *unpublished data*). *Atriplex,* therefore, is expected to be more sensitive to grazing by hares than *Artemisia.*

Patches of *Artemisia* grazed by hares in winter fully recovered; plant biomass was even significantly higher when grazed (Table 1A). Similarly, clipping shoots of *Artemisia* plants did not reduce resprouting relative to unclipped control plants. Patches of *Atriplex,* however, suffered from natural grazing by hares (Table 1B). Bushes that were clipped to the ground experimentally had very poor recovery. Removing single shoots of *Atriplex* did not affect resprouting when clipped late in February, but only 50% of shoots clipped in early April resprouted. Both mature and young *Atriplex* plants had very poor survival when clipped (Table 1B).

Brent Goose grazing pressure

In an experiment where we mimicked hare grazing by cutting down *Atriplex,* goose grazing pressure more than doubled relative to the untreated controls (Fig. 5A; WMP, $Z = -2.5$, $N = 25$, $P < 0.02$). Presence of food plants for Brent Geese was very similar between mowed and control plots (82% of the species were shared). Most palatable plants, however, were out of reach for geese when *Atriplex* was present, due to its rather dense structure.

Planting *Atriplex* bushes in the younger marsh caused a reduction in use of those sites by Brent Geese (Fig. 5B; WMP, $Z = -2.3$, $N = 9$, $P < 0.05$). Although important food plant species like *Puccinellia* continued to grow inside bushes, there were virtually no signs of grazing on those plants, confirming the interpretation that they were out of reach. A planted bush covered only one-quarter of the entire 4-m^2 plot. Reduction in goose grazing pressure was on the same order (29%),

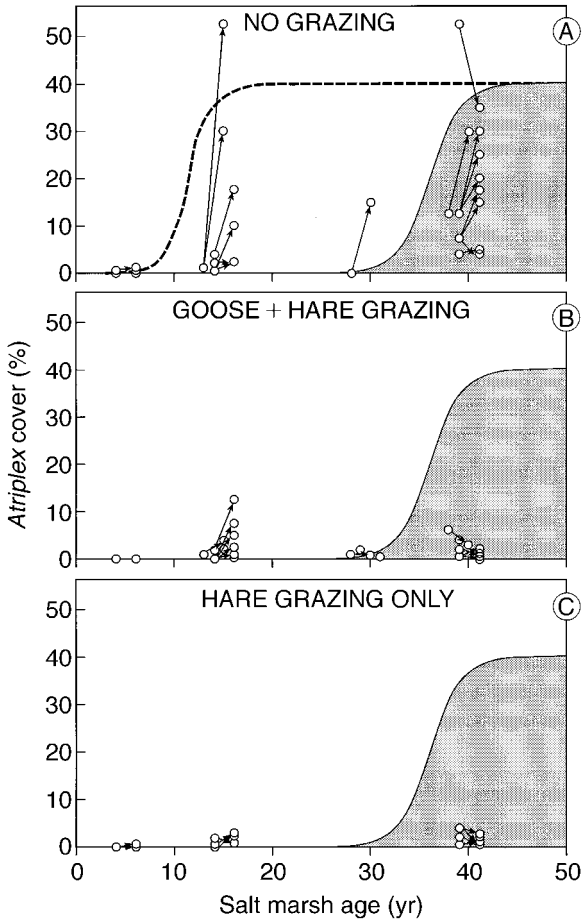

FIG. 3. Development of *Atriplex* cover in permanent plots in marsh parts of different developmental age in (A) the absence of grazing, (B) with goose and hare grazing, and (C) with hare grazing only. The stippled area in each panel depicts average cover of *Atriplex* as observed in the lower marsh ($Y = 40/[1 + \exp(-0.53X + 19.09)]$, $R^2 = 0.37$). The dashed line in (A) indicates expected cover of *Atriplex* in absence of hares. Arrows between small circles connect the plant cover estimates in the same plot over the study period.

indicating that the surface covered by *Atriplex* effectively was excluded from grazing by Brent Geese.

Atriplex and goose abundance

In the young salt marsh, communities characterized by *Atriplex* were rare (Fig. 6A), and found on creek banks only. During succession, *Atriplex* becomes more abundant and succession proceeds more rapidly in the absence of hares. In the older marsh, extensive areas were covered by *Atriplex* vegetation (Fig. 6A). In spring 1997, 49% of all Brent Geese were observed in *Limonium*-dominated vegetation (Fig. 6B). This narrow band fringing the Wadden Sea is crucial to the geese. Only 9% of the birds were recorded in *Atriplex* marshes. On the basis of the exclosure data, we expect that, in the absence of hares, vegetation dominated by *Limonium vulgare* will shift towards an *Atriplex*-dominated marsh within 10 yr rather than the 40 yr required when hares are present. Combining this with the assumption that new *Limonium* vegetation has arisen at a constant rate over the past 40 yr, it follows that the area of this *Limonium*-dominated vegetation would have been only a quarter of its present size, if no hares were present (17.5 ha). The area of *Atriplex* dominated vegetation would in that case be much larger, with 96 ha. This corresponds to a reduction in goose numbers of 44%, if densities of geese in the two vegetation types remained as observed in the 1997 census data.

DISCUSSION

This study presents evidence that hares facilitate Brent Geese by retarding vegetation succession. Winter grazing by hares prevented *Atriplex portulacoides* from becoming dominant in younger parts of the salt marsh, since *Atriplex* could poorly withstand removal of above-ground tissue. Goose grazing pressure decreased when bushes of *Atriplex* were planted, while removal of *Atriplex* swards led to an increase in goose utilization. In the absence of hares, a large part of the core feeding area of geese would be unsuitable for grazing by the birds. Additionally, hares reduced number of dead *Artemisia* stems in grassy swards, which otherwise might have hampered geese. Although hares were able to control *Atriplex* abundance in younger marshes, no negative effects of winter or spring grazing on *Artemisia* were established.

Geese, hares, and Atriplex

Geese have a poorly developed digestive system, and have to allocate a large part of their time to feeding to maintain a positive energy and nutrient balance (Bruin-

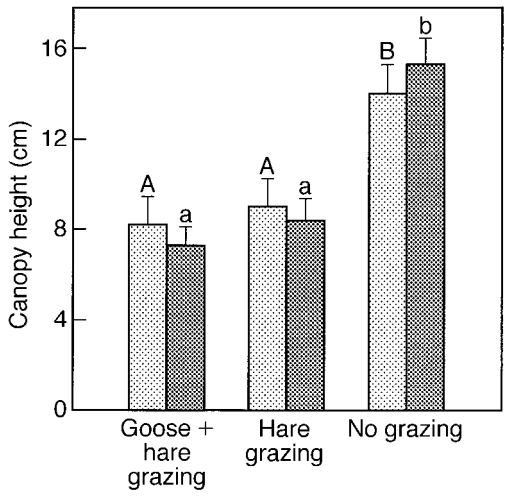

FIG. 4. Canopy height in plots dominated by *Festuca rubra* (light stippled) or *Artemisia maritima* (dense stippled) subject to different grazing regime. Plots were either grazed by geese and hares, grazed by hares only, or not grazed at all. Different letters indicate significant differences among the three treatments tested within a vegetation type.

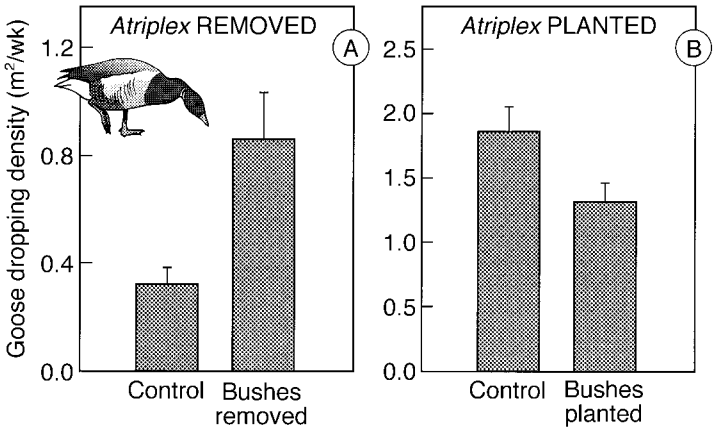

FIG. 5. Goose dropping density as a measure of goose visitation in experimental plots where *Atriplex* bushes were either removed (A) or planted (B). Removal experiments were performed in older marshes where goose grazing was low, whereas bushes were planted in the core feeding area of Brent Geese, which explains the difference in dropping density (in the control) between the two sites.

zeel et al. 1997). This makes geese very susceptible to components of the sward that impede foraging efficiency and therefore reduce daily food intake. In an experimental setup, Van der Wal et al. (1998) showed that a high fraction of standing dead material significantly reduced the intake rate of captive Barnacle Geese. In a study along the Dutch mainland coast, a low density of *Artemisia* in grassy swards was sufficient to reduce Brent Goose grazing (D. Kuiper, *personal communication*). Dead stems of *Artemisia* probably reduced accessibility of the sward. For the same reason, hares likely benefit Brent Geese by grazing down *Artemisia* in the Schiermonnikoog marsh in winter or early spring. Similarly, by grazing *Atriplex* down, hares keep the sward in suitable grazing condition for Brent Geese, thereby enhancing goose use.

During vegetation succession, taller plant species invade, which will outshade earlier successional species (Huisman et al. 1999, Tilman 1988). Grazing can alter the rate of plant species replacement (Crawley 1983). Although herbivory tends to hasten succession from shrubs and pioneer trees to forest, it typically retards succession from earlier seres (Davidson 1993). In the present study, hare grazing also retarded plant species replacement. During winter, hares switched from a diet dominated by grasses to a diet with a high proportion of woody species, similar to related species (Dodds 1960 [snowshoe hare, *Lepus americanus*], Gibbons et al. 1993 [black-tailed jackrabbit, *Lepus californicus*]). Actual proportion of woody species in the diet will largely depend on availability. In the young marsh, both *Atriplex* and *Artemisia* were scarce. Here hares fed primarily on grasses throughout the year, although substantial *Atriplex* consumption occured in winter. In the older marsh, where extensive *Atriplex* swards were common, >50% of the hare's winter diet consisted of that species.

With >65% fiber (as neutral detergent fiber, NDF) and <2% nitrogen (R. van der Wal, *unpublished data*), *Atriplex* has to be regarded as a low-quality food plant. The reason why hares do feed on the plant is likely the lack of alternative food sources. During winter, the majority of the graminoid standing crop is dead, or concealed in a dense mat of dead shoots (R. van der Wal, *unpublished data*). Belowground food sources are frequently out of reach due to frozen soil. Large-scale movements during periods of food scarcity due to extreme snow conditions are reported for hares in Siberia and southeastern Europe (Grzimek 1972). In our study area, hares were highly sedentary, spending the entire year in approximately the same area (P. Kunst, *personal communication*). By grazing on *Atriplex* in periods of food scarcity, hares have a profound effect on the marsh and its herbivores.

Communities dominated by *Salicornia* sp. and *Limonium vulgare* develop into *Atriplex* marshes over time (Roozen and Westhof 1985, Leendertse et al. 1997). On Schiermonnikoog, ~40 yr are required for *Atriplex* to reach dominance. In plots dominated by *Limonium vulgare,* exclusion of hares led to a rapid increase in *Atriplex* abundance. Although no exclosures were erected in the lower mashes where *Salicornia* sp. dominated, we expect an increase of *Atriplex* after hare exclusion here as well, due to its close association with both *Limonium* and *Salicornia* sp. (Chapman 1950). In the absence of hares, *Atriplex* is expected to be dominant in large parts of the lower marsh after ~10 yr of saltmarsh development, meaning that hares keep the sward suitable for goose grazing by delaying vegetation succession for >25 yr. Brent Geese, feeding mostly on *Puccinellia maritima* growing in the lower marsh, therefore either must shift to higher parts of the marsh, or leave the area if no hare grazing on *Atriplex* occurs. We calculated a reduction of ≥44% in carrying capacity of the marsh for Brent Geese in the absence of hares. However, we expect an even larger decrease in numbers if the core feeding area becomes unsuitable for goose grazing. Large parts of the marsh are now in use as a buffer area when food stock is temporarily depleted. Geese then use parts of the higher marsh but return to the *Limonium* vegetation to harvest regrowth of their

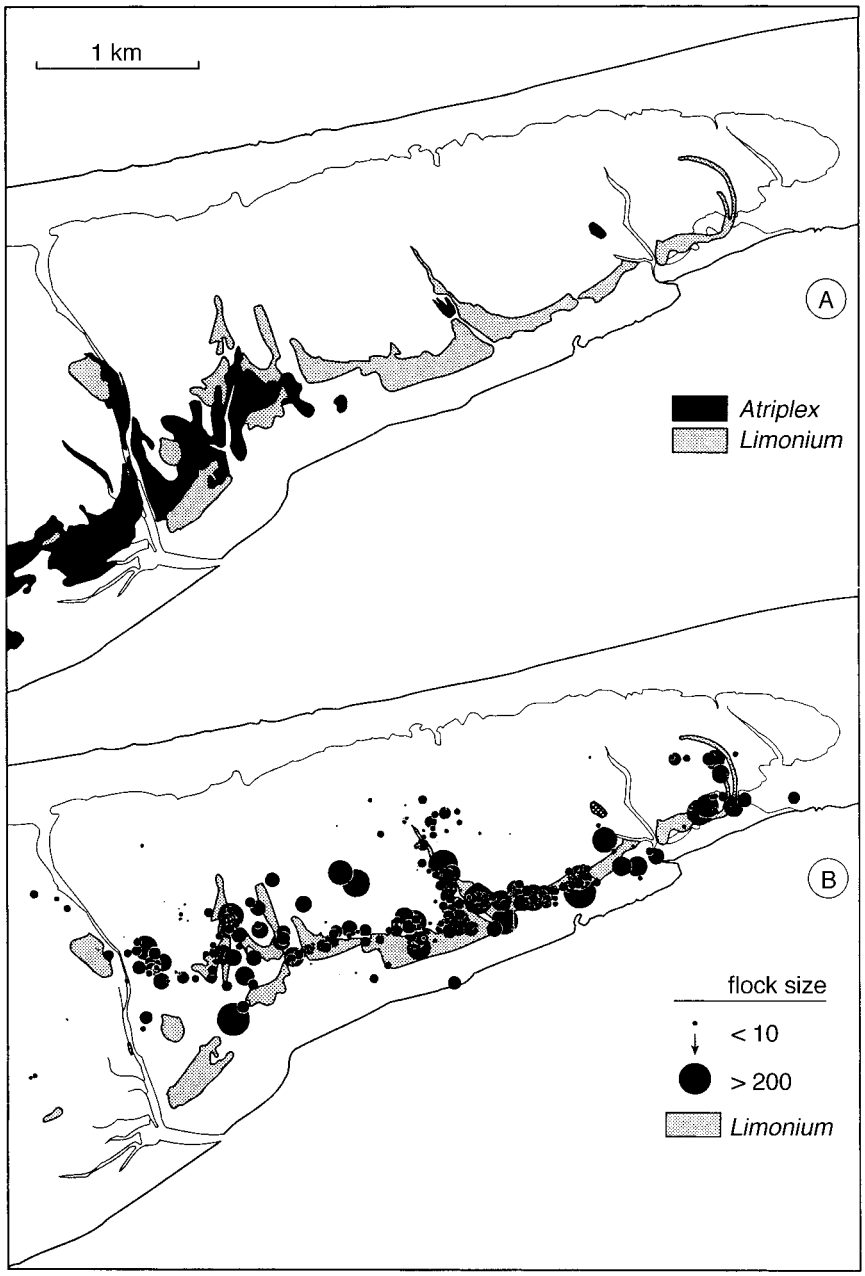

FIG. 6. (A) Incidence of *Atriplex*- and *Limonium*-dominated vegetation types on the eastern part of Schiermonnikoog and (B) distribution of Brent Geese in spring 1997 projected on *Limonium* dominated vegetation. In the absence of hares, *Limonium*-dominated vegetation is expected to change rapidly into *Atriplex*, which will lead to a reduction in suitable feeding grounds for Brent Geese. Youngest parts of the salt marsh are found in the east (right-hand side of figure), whereas older parts are in the west (left).

prime food plants (Prop and Deerenberg 1991, Drent and van der Wal 1999).

Hares losing control

Although hares effectively retarded vegetation succession, they were not able to prevent *Atriplex* from becoming the dominant plant, which can be attributed to several factors. First, hares might not influence rate of successional change in the high marsh to the same extent as they do in the low marsh. Successional changes in the higher marsh where hares graze during most of the year are likely to cause a decrease in local grazing pressure over time, resulting in too few hares to keep up with *Atriplex* development. During succession, the tall grass species *Elymus athericus* invades the higher marsh where it shades out more palatable grass-

es (Huisman and Olff 1998). Density of hares in dense *Elymus* swards is low (Van de Koppel et al. 1996, Huisman et al. 1999). Second, the geographical position of *Atriplex* fields might set the level of *Atriplex* utilization by hares. From a radiotelemetry study (R. van der Wal, *unpublished data*), we know that hares spent a large proportion of their time in dunes, especially during extreme high tides. It is unlikely that distance between the lower marsh and dunes, which is greatest in the older parts of the Schiermonnikoog marsh, causes reduced browsing of *Atriplex* in the lower marsh because home ranges of hares are sufficiently large to allow them to use both habitats. Third, population size in earlier years might have been too low to control *Atriplex.* Data on the population size of hares on the island are poor, but hunting records indicate that population size has not been much lower in earlier years, making it unlikely that fluctuation in population size is the cause of high *Atriplex* cover in the older marshes. Therefore, we expect invasion of later successional species in the higher marsh to be the most likely explanation for the loss of control by hares over the lower salt marsh.

Scaling up the importance of facilitation for spring-staging Brent Geese

In spring, the majority of the Brent Goose population utilize coastal salt marshes, from southern France to mid-Denmark (Cramp and Simmons 1977). The distribution of Brent Geese outside the breeding season markedly corresponds with the occurrence of *Atriplex portulacoides* (Meusel et al. 1965). In other words, in the lower salt marsh Brent forage in a zone where *Atriplex* can reach dominance. We claim that facilitation by herbivores has a large impact on the carrying capacity of the entire northwest European coast for Brent Geese, partly because much of the lower salt marsh would be dominated by *Atriplex portulacoides* in the absence of these herbivores (see also Van Wijnen and Bakker 1997).

Not only hares, but also other herbivores can prevent or delay *Atriplex* from becoming dominant. Rabbits are reported to graze down this plant species in marshes on the east coast of Britain (Chapman 1950); this has also been observed in Denmark (A. Jensen, *personal communication*). Furthermore, domestic cattle, sheep, and horses can keep *Atriplex* cover low. In the Camarque, southern France, exclusion of free-ranging horses from *Limonium*-dominated vegetation resulted in an increase in *Atriplex* cover (Bassett 1980). *Atriplex* is dominant in the French coastal marshes of Baie du Mont St. Michel, except where sheep grazing prevails and a short turf of *Puccinellia* is found (Vivier 1997). In grazed marshes in south Wales, *Atriplex* is found much less frequently and is mainly confined to the margins of creeks (Chapman 1950). Along the German coast, sheep grazing prevents *Atriplex* from outcompeting *Puccinellia* (Kiehl et al. 1996). In Schleswig-Holstein, northern Germany, sheep grazing pressure has been very intense during the last decades, resulting in a homogenous short and grassy vegetation that covered nearly 80% of the saltmarsh area (Stock 1993). Here, *Atriplex* cover is expected to be very low (cf. Kiehl et al. 1996). On Skallingen, Denmark, sheep and cattle keep out *Atriplex* (Jensen 1985), and this plant species was also largely controlled in the cattle-grazed part of the Schiermonnikoog marsh (Van Wijnen et al. 1997).

Atriplex appears to be sensitive to various sorts of physical damage, like trampling and grazing but also to compaction of the sediment (Chapman 1950, Jensen 1985). Since it is not likely that hares are capable of compacting the sediment, physical damage alone seems to be sufficient to control this plant species.

Few studies have related grazing effects of other herbivores to goose abundance. On Schiermonnikoog, cattle limit the abundance of tall growing plants like *Elymus athericus* and *Atriplex.* The maintenance of a grassy sward by summer grazing with cattle allowed extensive exploitation by both Brent Geese and Barnacle Geese (Olff et al. 1997, Huisman and Olff 1998). In Schleswig-Holstein, Barnacle Geese dropped sharply in numbers after a reduction in sheep grazing pressure (Bakker et al. 1997). Both goose species appear to prefer marshes with a short turf, realized by grazing with livestock (review in Bakker et al. 1997).

In general, grazing by livestock or by natural herbivores like hares and rabbits can prevent tall plant species from becoming dominant. Most mainland and island salt marshes are grazed by cattle or sheep. Furthermore, rabbits and hares are found on most of the Wadden Sea islands (Van Laar 1981) and mainland coast, where Brent Geese feed in marshes. Therefore, facilitation is expected to be of utmost importance to Brent Geese and will largely set the carrying capacity along the northwestern European coastline for this goose species.

We are not aware of other data on natural herbivores influencing grazing conditions for geese in the northwestern European marshes. In former times, several species of deer and members of the bovid family might have enforced similar patterns now induced by livestock, but evidence is lacking.

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